

Lamina architecture and anatomy in the Heliconiaceae and Musaceae (Zingiberales)

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Abstract:

Lamina size, thickness, venation, and anatomy are studied in 15 species of *Heliconia* (Heliconiaceae), 3 species of *Musa*, and 1 of *Ensete* (Musaceae). The most typical laminae of these genera are large and oblong and have an acute or irregular apex and an asymmetrical cordate base. The laminar veins are parallel and are oriented essentially perpendicular to the costa and the margin. However, there is considerable variation in lamina architecture in the Heliconiaceae. Thickness ranges considerably across the lamina, with considerable variation between species. The only pattern common to all species is that the blades are thinner at the margin than at the costa. The veins of the lamina occur in a number of size classes that are arranged into a repeating unit called a set. Set patterns are described for the species and families. Although the Heliconiaceae and Musaceae do not differ in general set pattern, variation in the Heliconiaceae tends toward simpler sets, whereas the Musaceae tends towards more complex sets. Lamina anatomy is similar to that reported in the literature for these families, with several notable exceptions. The Heliconiaceae and Musaceae may be distinguished by characteristics of their lamina anatomy and by the fact that Musaceae blades have an irregular apex. The value of these characters for taxonomic and cladistic analyses is discussed. Key words: leaves, plant anatomy, vasculature, Zingiberales, Musaceae, Heliconiaceae.

Les auteurs ont étudié la dimension du limbe, l'épaisseur, la venation et l'anatomie de la feuille chez 15 espèces d'*Heliconia* (Heliconiaceae), trois *Musa* spp. et une *Enseta* sp. (Musaceae). Les limbes les plus typiques chez ces genres sont grands, oblongs et présentent un apex acuminé ou irrégulier ainsi qu'une partie basale asymétrique et cordée. Les veines du limbe sont parallèles et s'orientent de façon essentiellement perpendiculaire à la nervure centrale et à la marge. Cependant, il y a une forte variation dans l'architecture du limbe chez les Héliconiaceae. L'épaisseur fluctue considérablement d'une partie à l'autre du limbe et varie beaucoup selon les espèces. Le seul patron commun à toutes les espèces, c'est que leurs limbes sont plus minces à la marge qu'au voisinage de la nervure centrale. Les nervures du limbe appartiennent à un nombre de classes dimensionnelles qui sont disposées selon une unité répétitive appelée ensemble. Les auteurs décrivent les patrons de ces ensembles pour les espèces et les familles. Bien que le patron général des ensembles ne diffère pas chez les Héliconiaceae et les Musaceae, la variation observée chez les Heliconiaceae tend vers des ensembles plus simples, alors que chez les Musaceae, la tendance favorise les ensembles plus complexes. L'anatomie du limbe est conforme à celle présentée dans la littérature pour ces familles, avec cependant des exceptions.

remarquables. On peut distinguer les Heliconiaceae et les Musaceae par les caractéristiques anatomiques de leur limbe et par le fait que les limbes foliaires des Musaceae présentent un apex irrégulier. Les auteurs discutent la valeur de ces caractères pour l'analyse taxonomique ou cladistique. Mots clés : feuilles, anatomic, végétale, vascularisation, Zingiberales, Musaceae, Heliconiaceae.

Article:

INTRODUCTION

The Heliconiaceae and Musaceae are two families of the Zingiberales, the order of tropical monocotyledons that includes the bananas and the gingers. Although the most important characters in the supergeneric classification of this order have been drawn from inflorescence and floral morphology (Schumann 1900; Dahlgren et al. 1985), many vegetative characters have also been shown to be useful. For instance, phyllotaxis, rhizome type, and trichome structure have been used (Tomlinson 1961; Dahlgren and Rasmussen 1983).

Although often neglected in higher level classification, leaves are potentially a rich source of taxonomic characters. This neglect has been especially prevalent in the monocotyledons. Relatively, few monocotyledon leaf characters have been analyzed and presented in a form suitable for cladistic analysis. The typical conception of the architecture of a monocotyledon leaf blade, such as one encounters in an undergraduate morphology, anatomy, or taxonomy textbook, is of a simple blade with parallel venation. This type of description implies an absence of complex leaf architecture, an implication that is unmerited, at least in the Zingiberales.

In the Zingiberales, a few leaf characteristics have been mentioned in the literature as potentially being of taxonomic use. Hickey and Peterson (1978) proposed identifying blades of the Zingiberaceae (ginger family) on the basis of size differences among the vascular bundles in the lamina. They found that these size differences occur in a patterned fashion in many species. This quality of the veins permits them to be described with a pattern or formula, which Hickey and Peterson (1978) referred to as a set. Tomlinson (1959, 1969) investigated leaf anatomy as part of his study of the anatomy of the Zingiberales and listed eight characters that are found only in *Heliconia* and eight that are found only in *Musa*. Frolich and Barthlott (1988) suggested the use of epicuticular wax patterns as a character for use in determining the phylogeny of the monocotyledons. They found *Strelitzia*-type wax in many species of the Zingiberales.

An additional leaf characteristic of potential taxonomic value is the occurrence of lamina tearing or splitting, the process by which simple leaves become falsely compound, emulating the leaves of palms (Skutch 1927). Leaf tearing occurs in many,

TABLE 1. Species investigated

| Species | Collector and voucher | Deposited* | Accession No.† |
|--|-----------------------|------------|----------------|
| Heliconiaceae | | | |
| Subgenus <i>Griggsia</i> | | | |
| Longa group | | | |
| <i>Heliconia stilesii</i> Kress | — | — | W 85P297 |
| | Kirchoff 89-260 | BISH | W 82P522 |
| Pendula group | | | |
| <i>Heliconia pendula</i> Wawra | Kirchoff 89-241 | BISH | W 75P1200 |
| Platystachys group | | | |
| <i>Heliconia platystachys</i> Baker | — | — | W 81P682 |
| | — | — | W75P1196 |
| | — | — | W 85P255 |
| <i>Heliconia chartacea</i> Lane ex. Brreiros | Kirchoff 89-253 | BISH | W 82P815 |
| | — | — | L85.0112 |
| Subgenus <i>Heliconia</i> | | | |
| Section <i>Heliconia</i> | | | |
| <i>Heliconia caribaea</i> Lam. | Kirchoff 89-234 | BISH | W 78P276 |
| <i>Heliconia caribaea</i> × <i>bihai</i> | Kirchoff 89-243 | BISH | W 78P259 |
| <i>Heliconia stricta</i> Huber | Lau 2858 | BISH | W 75P1186 |
| <i>Heliconia bourgaeana</i> Petersen | Kirchoff 89-246 | BISH | W 86P278 |
| Section <i>tortex</i> | | | |
| <i>Heliconia latispatha</i> Benth. | Kirchoff 87-107 | BISH | W 74P1142 |
| Subgenus <i>Stenochlamys</i> | | | |
| Section <i>cannastrum</i> | | | |
| <i>Heliconia metallica</i> Pl. & Lind. ex. Hook | Kirchoff 89-236 | BISH | W 75P57 |
| | Kirchoff 89-252 | BISH | W 85P301 |
| <i>Heliconia vaginalis</i> Benth. | Lau 2668 | BISH | W 75P1187 |
| <i>Heliconia vaginalis</i> Benth. ssp. <i>mathiasiae</i> (Dan. & Stil.) Anders | Kirchoff 89-247 | BISH | W 81S954 |
| Section <i>stenochlamys</i> | | | |
| <i>Heliconia psittacorum</i> L. f. | Kirchoff 87-111 | BISH | W 76P779 |
| | Kirchoff 89-258 | BISH | W 82P142 |
| Section <i>zingiberastrum</i> | | | |
| <i>Heliconia hirsuta</i> L. f. | Lau 2664 | BISH | W 74P133 |
| Subgenus <i>Heliconiopsis</i> | | | |
| <i>Heliconia indica</i> Lam. | Kirchoff 87-109 | BISH | W 79P1202 |
| | Lau 2757 | BISH | W 83P116 |
| | Kirchoff 89-256 | BISH | W 83P119 |
| Musaceae | | | |
| <i>Musa rosea</i> Hort. ex Baker | Kirchoff 87-116 | BISH | W 77P550 |
| <i>Musa velutina</i> | Kirchoff 88-144 | HLA | L 67.0284 |
| <i>Musa</i> cv. Go Sai Yung | Kirchoff 87-115 | BISH | W 82P86 |
| <i>Musa</i> sp. | Kirchoff 88-147 | HLA | L 86.0577 |
| <i>Ensete</i> sp. | — | — | W 77S1 |

*Abbreviations of herbaria according to Holmgren et al. (1981).

†W, Waimea Arboretum, Oahu, Hawaii; L, Lyon Arboretum, Oahu, Hawaii.

but not all, of the plants of the Zingiberales, suggesting that taxonomic information can be gained through a systematic study of this phenomena.

There are three main goals of this paper. First, we demonstrate a degree of architectural complexity and variation in the leaf blades of the Heliconiaceae (*Heliconia*) and Musaceae (*Musa*, *Ensete*) not usually associated with monocotyledons. Second, we investigate the taxonomic usefulness of Hickey and Peterson's (1978) ideas, especially their usefulness in a cladistic study. Third, this study forms the basis for a statistical analysis of leaf tearing in *Heliconia* currently underway in the second author's laboratory. Architectural features of the leaf blade, including size, shape, thickness, and vein arrangement, are examined in this regard. We

also verify and extend Tomlinson's (1969) observations of the anatomical features of lamina anatomy and discuss the use of these characters in a cladistic analysis of the order.

MATERIALS AND METHODS

Leaf blades and voucher specimens were collected from Lyon and Waimea arboretums, Oahu, Hawaii (Table 1). Specimens were either pressed and dried or portions of the blade were preserved in formalin — acetic acid — alcohol (FAA) (Berlyn and Miksche 1976).

Blade lengths and widths were measured in the gardens from live plants using a tape measure marked in inches. The measurements were later converted to centimetres. In the Heliconiaceae, the lamina base is typically oblique, with one side of the blade attached to the petiole higher than the other (Fig. 1A). Length was measured from the apex to the farthest point at which the blade attaches to the petiole. Width was measured across the lamina at the widest point in the

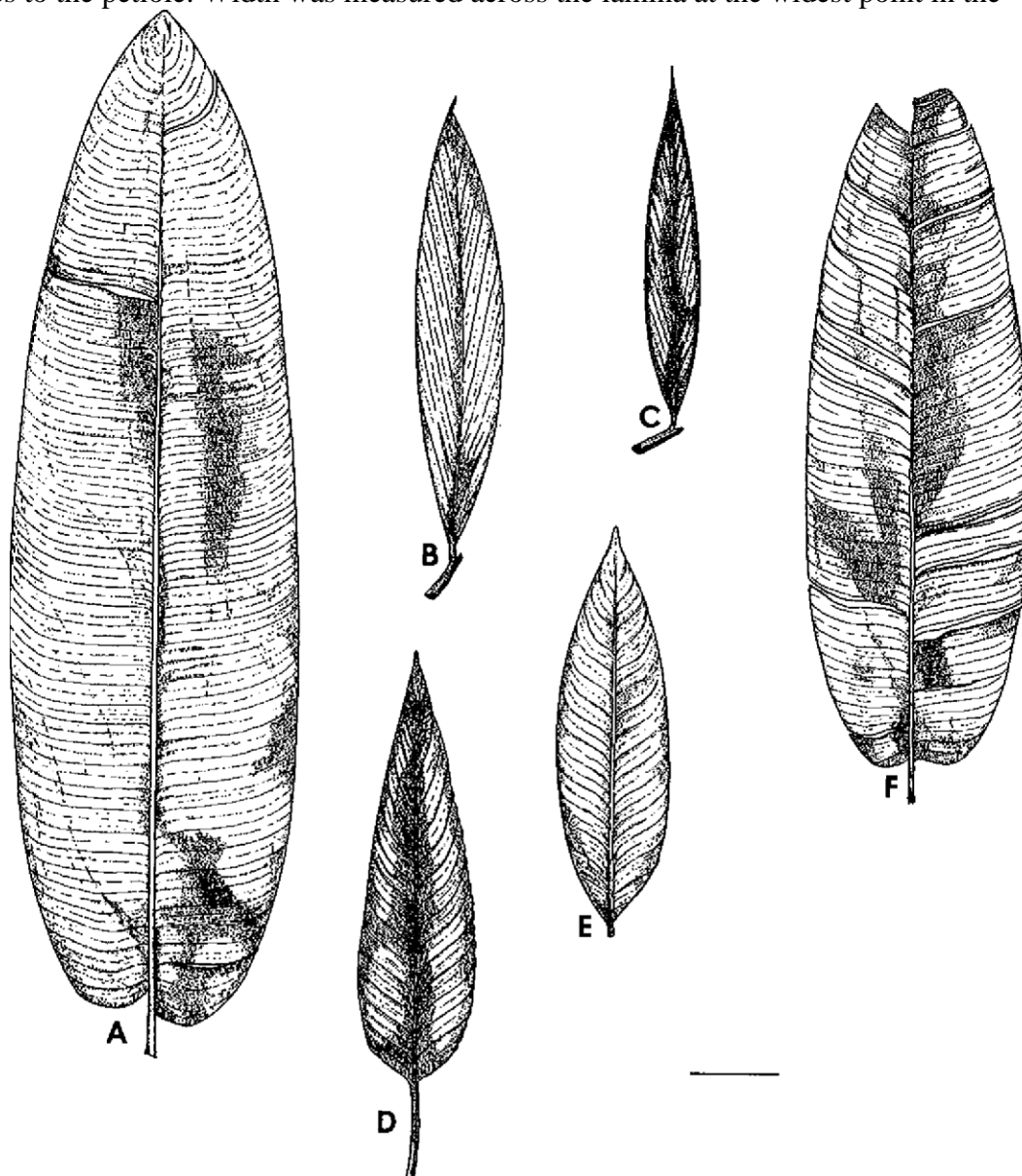


FIG. 1. Leaf blades. (A) *Heliconia platystachys* (type 1). (B) *Heliconia psittacorum* (type 2). (C) *Alpinia calcarata*. (D) *Strelitzia reginae*. (E) *Heliconia vaginalis* ssp. *mathiasiae* (type 3). (F) *Musa velutina*. Scale bar = 20 cm.

region midway between the apex and base of the blade. At least five measurements of length and width were made from each plant. Only mature foliage leaves were measured. The leaves selected represent the variation in a ramet, not a genet.

The thicknesses of the blades were measured in the field using a vernier caliper, calibrated in millimetres. Thickness measurements were taken in two fashions at six locations on the blades: perpendicular (i.e., at right angles to the longitudinal course) and parallel to (i.e., between) the veins; at the costa and margin; and apically, medially, and basally (Fig. 2). The proportional thicknesses of the palisade and spongy mesophyll were determined from linear measurements of these regions in cross sections of leaf blades. Proportions of the lamina thickness devoted to palisade and spongy mesophyll were obtained by dividing the thicknesses of these regions by the thickness of the lamina measured from cross sections.

Vein angles were measured from fresh blades in the field and from dried blades in the laboratory using a 10x ocular comparator with a redicle graduated in degrees. Angles were measured at three distinct locations where the veins typically change orientation. These angles are (i) the costal angle, where the laminar veins merge with the costa; (ii) the laminar angle, the angle between the laminar veins and the costa at the center of the blade; and (iii) the marginal angle, where the laminar veins merge with the marginal vein (Fig. 3).

Cross sections of the leaf blades of 13 species were prepared for anatomical study using standard paraffin techniques (Berlin and Miksche 1976). Species were selected for study so as to overlap as little as possible with those studied by Tomlinson (1959, 1969). Pieces of leaves were collected from a standard location at the center of the blade, midway between the apex and the base and equidistant from the margin and the costa. In some species, pieces closer to the costa and margin were also studied. The selected pieces were softened in 4-7% ethylcneidamine (Carlquist 1982) for 5-21 days, dehydrated in 2,2-dimethoxypropane (Postek and Tucker 1976), and transferred to tertiary butyl alcohol before embedding in Tissue Prep 2. Vacuum was used at all stages. Sections were cut on a Reichert 2040 Autocut at 8-16 μ m. Sections were dewaxed using ClearRite III in place of xylene, stained in safranin and fast green (Berlin and Miksche 1976) or safranin and alcian green (Joel 1983), and mounted in Permount.

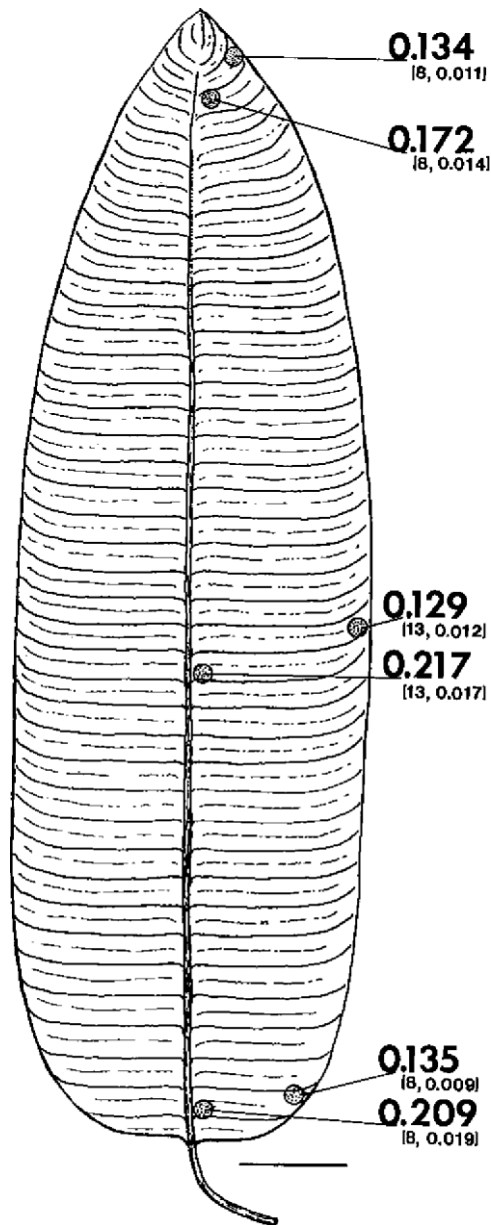


FIG. 2. *Heliconia chartacea* lamina, showing site of measurements and thickness in millimetres. Values in parentheses are number of measurements and standard deviation.) Scale bar = 20 cm.

Additional fixed material was transferred to 95% EtOH and hand sectioned, either freehand or on a cylinder microtome. In both cases the leaf blade was held between two pieces of carrot to provide support. Aqua-poly mount (Polysciences, Inc., Warrington, PA) was used to mount these sections.

Clearings were prepared according to indications given by O'Brien and McCully (1981). Dry leaf material was rehydrated by soaking in hot water for ca. 1 h followed by 50% EtOH for ca. 24 h. FAA- preserved material was washed in water. After the initial treatment the blades were placed in 50-70% EtOH in a hot water bath, followed by 5% NaOH for 1-3 days. The cleared leaves were left unmounted and observed under an Olympus SZH stereo microscope or a Wild MI I compound microscope on temporary slide mounts. Measurements of vein width were made with

an ocular micrometer on one of these microscopes. Untreated fresh and dry blades were examined using the Olympus stereomicroscope with raking illumination.

The venation formulas of the blades were determined based on a modification of a system proposed by Hickey and Peterson (1978).

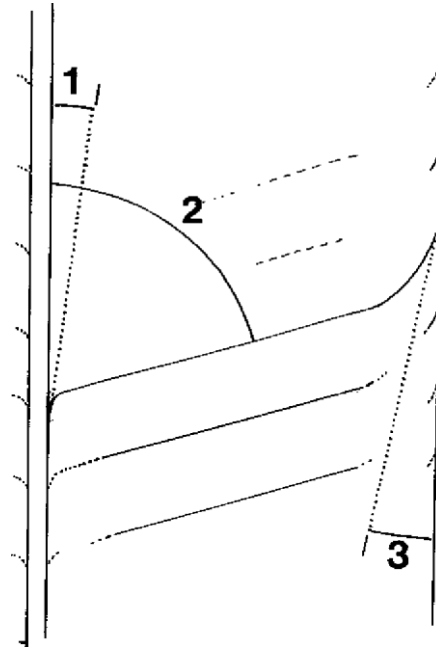


Fig. 3. Sites of angle measurements. 1, costal angle; 2, laminar angle; 3, marginal angle. The arrow indicates direction to lamina apex.

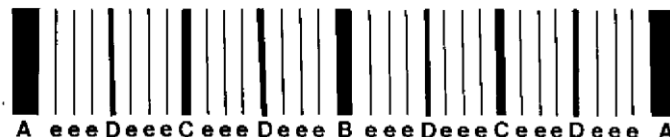


FIG. 4. Diagrammatic representation of a vein set in the Heliconiaceae. A, B, C, D, and e are the vein subsets.

In the Zingiberales the parallel veins of the lamina usually occur in size classes that are arranged in relatively uniform patterns across the blade (Fig. 4). Hickey and Peterson (1978) refer to each size class as a subset and call the whole pattern a set. Hickey and Peterson identify the subsets by the width of the veins. Subset A, for instance, is composed of those veins from 0.25 to 0.3 mm wide. The dimensions of a subset are thus constant across all leaves. Instead of using absolute subsets, we designate the largest laminar veins in a given blade the A veins, the second largest the B veins, etc. The smallest subset in a given blade is represented, both by Hickey and Peterson (1978) and ourselves, by a lowercase letter. In this way we produce a relative ranking of the subsets for each species. Set patterns were determined from a standardized position on each lamina: midway between the apex and the base of the lamina, near, but not directly adjacent to the costa.

The terminology of Hickey (1973) is used to describe the shape of the blades.

RESULTS

Heliconiaceae

The leaf blades of the Heliconiaceae have a diversity of shapes and sizes. Most of the blades share a common mor-

TABLE 2. Leafsize (\pm SD) and type for species investigated

| Species | Type | N | Length* (cm) | Width* (cm) | Source of data† |
|---|------|----|------------------|----------------|-----------------|
| Heliconiaceae | | | | | |
| <i>Heliconia stilesii</i> | 1 | 5 | 138.4 \pm 23.9 | 40.5 \pm 4.0 | DL |
| <i>Heliconia pendula</i> | 1 | | 160 | 30 | Schumann 1900 |
| <i>Heliconia platystachys</i> | 1 | 10 | 114.0 \pm 22.7 | 34.2 \pm 5.4 | DL, FL |
| <i>Heliconia chartacea</i> | 1 | 12 | 76.8 \pm 17.7 | 24.1 \pm 4.8 | FL |
| <i>Heliconia caribaea</i> | 1 | 5 | 181.6 \pm 32.0 | 46.2 \pm 5.1 | FL |
| <i>Heliconia caribaea</i> \times <i>bihai</i> | 1 | | 100 | 45 | Andersson 1981 |
| <i>Heliconia stricta</i> | 1 | | 100 | 29 | Andersson 1981 |
| <i>Heliconia bourgaeana</i> | 1 | | — | — | DL |
| <i>Heliconia latispatha</i> | 1 | | 150 | 30 | Andersson 1985 |
| <i>Heliconia metallica</i> | 1 | 5 | 83.4 \pm 12.7 | 18.4 \pm 2.0 | DL, FL |
| <i>Heliconia vaginalis</i> | 3 | 5 | 68.2 \pm 11.6 | 11.4 \pm 2.4 | FL |
| <i>Heliconia vaginalis</i> ssp. <i>mathiasiae</i> | 3 | | — | — | DL |
| <i>Heliconia psittacorum</i> | 2 | 5 | 45.3 \pm 1.9 | 10.8 \pm 0.6 | FL |
| <i>Heliconia hirsuta</i> | 3 | | 40 | 14 | Andersson 1985 |
| <i>Heliconia indica</i> | 1 | 10 | 144.0 \pm 32.4 | 45.1 \pm 5.0 | DL, FL |
| Musaceae | | | | | |
| <i>Musa rosea</i> | 1 | | — | — | DL |
| <i>Musa velutina</i> | 1 | 20 | 90.2 \pm 18.1 | 30.4 \pm 5.0 | FL |
| <i>Musa</i> cv. Go Sai Yung | 1 | | — | — | DL |
| <i>Ensete</i> sp. | 1 | | — | — | DL |
| <i>Musa</i> sp. | 1 | | — | — | DL |

*The usual upper limit of blade size is reported from the literature; unusually large or small leaves are excluded.

†DL, dry lamina; FL, fresh lamina.

phology, but with a number of notable deviations from the standard. The typical lamina is oblong to more commonly narrowly oblong, with an asymmetrical, cordate base (Fig. 1A) and an acute to slightly acuminate apex. However, oblong, elliptic, narrowly elliptic, ovate, and lanceolate blades are found in the genus (Figs. 1B, 1E). The lamina apex occasionally forms a right angle, as in *Heliconia stilesii*, or is obtuse as in *Heliconia indica*. The shape of the lamina base shows the greatest variability. In various species it is asymmetrically acute, decurrent obtuse, decurrent acute, symmetric and rounded, or asymmetric cuneate.

Blade size in the family varies from small blades, of sizes similar to those typically found in the Zingiberaceae and related families, to sizes approximating the larger blades of the Musaceae (Table 2). Typically, *Heliconia* blades are large. A common size, for instance in *Heliconia platystachys*, is ca. 114 cm long x 34 cm wide. *Heliconia caribaea* has distinctly larger than average leaves, with a blade size on the order of 182 x 46 cm. At the other extreme, the blades of *Heliconia psittacorum* are ca. 45 x 11 cm, distinctly smaller than usual. Those plants having a musoid growth habit (Andersson 1981) tend to have larger blades, whereas those of the cannoid and zingiberoid habits (Andersson 1981) tend towards smaller sizes. However, growth habit is

not a reliable indicator of blade size. The aforementioned *H. psittacorum* is a plant of musoid habit.

The length (L) to width (W) ratio of the blade is variable across the Heliconiaceae, with no apparent correlation with other characteristics of the leaves. The range of L:W ratios in the study species is from 3:1 in *H. indica* to 6:1 in *Heliconia vaginalis* and *H. psittacorum*.

The thickness of the lamina is quite variable in the Heliconiaceae, both between species and within the blade of a single leaf. For instance, average thickness between the veins ranges from 0.167 mm in *Heliconia chartacea* to 0.303 mm in *H. caribaea* (Table 3, mean thickness parallel to veins). The variation in thickness across a single lamina is also considerable. The following general statements describe the variability in lamina thickness observed in the family. Thickness between the veins is used throughout. Thickness increases across the lamina from the margin to the costa, at all locations, in all species. The thickness of the lamina varies longitudinally in different ways in different species. Near the margin, blade thickness increases from the apex to the base in *H. platystachys*, *H. indica*, *H. vaginalis*, *H. stilesii*, and *H. caribaea*; decreases from the apex to the base in *H. psittacorum*; increases from the apex to the middle of the lamina then decreases to the base in *Heliconia metallica*; or decreases from the apex to the middle of the lamina then increases to the base in *H. chartacea*. Near the costa, blade thickness increases from the apex to the base in *H. platystachys* and *H. vaginalis* or increases from the apex to the middle of the lamina then decreases to the base in *H. indica*, *H. chartacea*, *H. metallica*, *H. psittacorum*, *H. stilesii*, and *H. caribaea*.

The vasculature of the blade consists of a costa, or midrib, laminar veins, which traverse the blade from the costa to the margin (or apex in some species), and often, though not always well defined, a marginal vein into which the laminar veins merge. The vasculature can be characterized by the costal, laminar, and marginal angles and thus by the course of the veins across the leaf blade (Fig. 3; Table 3).

The course of the veins typically changes drastically from the costa to the margin (Table 3). For instance, *H. chartacea* has a costal angle of 3.6°, a laminar angle of 75.2°, and a marginal angle of 4.8° (Table 3). *Heliconia psittacorum* is an exception to this rule, with a costal angle of 2.2°, a laminar angle of 12.3°, and a marginal angle of 7.8°. In this case the change in vein angle is relatively slight between the costa and margin.

The laminar angle discriminates best among the different blade architectures in the Heliconiaceae (Table 3). This angle is typically near 90°. The range is from 11.7° in *H. psittacorum* to 89.2° in *H. stilesii* (Table 3). Since both of these species

TABLE 3. Mean leaf thickness (mm \pm SD) and vein angles ($^{\circ}$ \pm SD) for species investigated

| Species | Thickness | | | Angle | | | |
|---|-----------|------------------------|--------------------|-------|----------------|-----------------|----------------|
| | N | Perpendicular to veins | Parallel to veins | N | Costal | Laminar | Marginal |
| Heliconiaceae | | | | | | | |
| <i>Heliconia stilesii</i> | 5 | 0.317 \pm 0.022 | 0.244 \pm 0.012 | 4 | 4.5 \pm 1.3 | 89.2 \pm 1.5 | 10.0 \pm 1.4 |
| <i>Heliconia pendula</i> | | — | — | 5 | 6.0 \pm 1.9 | 68.2 \pm 0.4 | 5.0 \pm 1.7 |
| <i>Heliconia platystachys</i> | 10 | 0.262 \pm 0.025 | 0.209 \pm 0.009 | 4 | 4.8 \pm 0.4* | 85.8 \pm 2.6 | 3.5 \pm 0.6 |
| <i>Heliconia chartacea</i> | 13 | 0.220 \pm 0.025 | 0.167 \pm 0.009 | 4 | 3.6 \pm 1.1* | 75.2 \pm 4.2 | 4.8 \pm 1.5 |
| <i>Heliconia caribaea</i> | 5 | 0.357 \pm 0.031 | 0.303 \pm 0.014 | 4 | 5.0 \pm 0.0 | 76.5 \pm 1.0 | 3.0 \pm 0.8 |
| <i>Heliconia caribaea</i> \times <i>bihai</i> | | — | — | 5 | 6.1 \pm 1.0 | 80.8 \pm 2.2 | 5.4 \pm 1.9 |
| <i>Heliconia stricta</i> | | — | — | 5 | 2.6 \pm 0.9 | 72.6 \pm 0.5 | 3.0 \pm 1.4 |
| <i>Heliconia bourgaeana</i> | | — | — | 5 | 7.4 \pm 3.4 | 81.0 \pm 1.6 | 9.4 \pm 1.8 |
| <i>Heliconia metallica</i> | 5 | 0.321 \pm 0.009 | 0.267 \pm 0.010 | 4 | 4.5 \pm 0.6 | 82.5 \pm 1.0 | 12.2 \pm 1.7 |
| <i>Heliconia vaginalis</i> | 5 | 0.297 \pm 0.021 | 0.270 \pm 0.023 | 4 | 3.2 \pm 0.5 | 35.8 \pm 3.4 | 4.0 \pm 0.8 |
| <i>Heliconia psittacorum</i> | 5 | 0.225 \pm 0.018 | 0.206 \pm 0.017 | 4 | 2.2 \pm 0.5 | 11.7 \pm 2.2 | 7.8 \pm 1.9 |
| <i>Heliconia hirsuta</i> | | — | — | 6 | 4.3 \pm 1.5 | 49.5 \pm 4.9 | 3.2 \pm 1.0 |
| <i>Heliconia indica</i> | 10 | 0.343 \pm 0.033 | 0.286 \pm 0.029 | 8 | 3.5 \pm 1.2 | 81.4 \pm 10.7 | 2.8 \pm 0.5 |
| Musaceae | | | | | | | |
| <i>Musa rosea</i> | | — | — | 5 | 4.7 \pm 0.4 | 70.4 \pm 2.3 | 10.8 \pm 2.4 |
| <i>Musa velutina</i> | 20 | 0.305 \pm 0.024 | 0.260 \pm 0.014† | 5 | 4.1 \pm 0.5 | 74.2 \pm 0.4 | 19.6 \pm 9.8 |
| <i>Musa</i> sp. | | — | — | 5 | 9.4 \pm 0.5 | 81.2 \pm 4.4 | 16.0 \pm 2.9 |

*N = 5.

†N = 10.

are of musoid habit (Andersson 1981), vein angle is not necessarily correlated with growth form. Plants that bear smaller laminas, such as *H. psittacorum*, *H. vaginalis*, and *H. hirsuta*, have laminar angles of less than 50°. Species with large laminas tend to have larger costal angles (ca. 75-85°), as observed in *H. stilesii*, *H. platystachys*, *H. chartacea*, *H. caribaea*, *H. caribaea* \times *bihai*, *H. stricta*, *H. metallica*, *H. indica*, and *H. bourgaeana*. *Heliconia pendula* is an exception to this rule. It has large blades with a laminar angle of 68.2°.

The costal angle and the marginal angle also vary among the species of *Heliconia*, however, there is less variability in these angles (Table 3). The range of variation within a single species is illustrated by *H. chartacea*. In this species, the costal angles range between 2.8 and 3.6°, and the marginal angles between 4.6 and 6.4°. In the whole family, the range of costal angles is from 2.2° in *H. psittacorum* to 4.5° in *H. metallica*; the range of marginal angles is from 2.8° in *H. indica* to 12.2° in *H. metallica*.

The laminas of *H. platystachys* are typical for the Heliconiaceae and can serve as a reference for the typical *Heliconia*-like leaf, which we designate type 1 (Fig. 1A; Table 2). The laminas of this species are oblong and have an acute apex and an asymmetrically cordate base. The laminar veins are parallel and are oriented essentially perpendicular to the costa and the margin.

Two other lamina types are found in the Heliconiaceae (Table 2). Type 2 consists of small laminas such as those of *H. psittacorum* (Fig. 1B), which are narrowly elliptic rather than oblong and have an acute base and apex. In type 2 laminas, the laminar veins are roughly parallel to the margin (laminar angle ca. 11.7°) rather than being perpendicular to it. This morphology is similar to that of the common blade form found in the Zingiberaceae (cf. *Alpinia calcarata*, Fig. 1C). *Heliconia psittacorum* is the single species we examined of this type. Type 3 laminas are symmetric and narrowly elliptic, with an acute apex and an asymmetric, acutely decurrent base. The laminar angle is ca. 36° (Table 3). By virtue of these features, type 3 laminas resembles

those of *Strelitzia reginae* (Strelitziaceae), the Bird of Paradise (Fig. 1D). Typical examples of this lamina type are found in *H. vaginalis* and *H. vaginalis* ssp. *mathiasiae* (Fig. 1E). *Heliconia hirsuta* may also be included in type 3 based on a laminar angle of 49°. However, this species is distinct among the plants observed in this study in having an ovate to lanceolate laminar shape and a rounded base.

The laminar veins of the Heliconiaceae occur in a number of size classes. For instance, in *Heliconia indica* the width of the vascular bundles ranges from 0.030 to 0.136 mm. Variation in vein size is not random but occurs in a patterned sequence across the leaf blade. This pattern may be expressed as a formula, representing the unit that is indefinitely repeated across the blade. This formula consists of two members of the largest vein class, which serve as endpoints, and all the veins that occur between these two. Hickey and Peterson (1978) call this unit of veins a set. The rule we adopt for coding the veins within a set is to name them alphabetically, such that the largest vein in a given species receives an uppercase A, the next largest B, and so on, until the smallest subset is named, for which a lowercase character is used. In this manner, a formula such as AcBcA is generated, describing a condition in which each primary vein is separated from the next by a tertiary-secondary—tertiary vein sequence.

There is considerable variation in vein set patterns both within a blade and between species. Local variations in the set are common within a leaf blade. These variations can occur for numerous reasons, such as the diminishing size of the veins approaching the margin, the presence of nonpatterned accessory veins near the costa, and numerous anomalies that occur in the set at sites near the apex and the base of the lamina. For example, a species with a partial formula of eeeDeee may be dddddd near the margin where the size of the D veins has diminished, and fEfDfEf adjacent to the costa where the veins are more differentiated in size. The number of e (or f) veins may vary between adjacent subsets (e.g., DeeeeCeeeD) or even

TABLE 4. Summary of set patterns for species investigated

| Species | Set pattern | | Source* |
|--|-------------------|-----------------------------|------------|
| | Subset formula | x | |
| Heliconiaceae | | | |
| <i>H. stilesii</i> | AxDxCxDxBxDxCxDxA | 3-8 e | DL, XS |
| <i>H. pendula</i> | AxCxBxCxA | 7-15 d | DL, XS |
| <i>H. platystachys</i> | AxDxCxDxBxDxCxDxA | 2-4 e | DL, XS |
| <i>H. chartacea</i> | AxDxCxDxBxDxCxDxA | 3-5 c | CL, DL, XS |
| <i>H. caribaea</i> | AxDxCxDxBxDxCxDxA | 2-4 e | CL, DL, XS |
| <i>H. caribaea</i> × <i>bihai</i> | AxDxCxDxBxDxCxDxA | 3-7 e | DL, XS |
| <i>H. stricta</i> | AxDxCxDxBxDxCxDxA | 1-4 c | DL, XS |
| <i>H. bourgaeana</i> | AxDxCxDxBxDxCxDxA | 2-4 e | DL |
| <i>H. latispatha</i> | AxDxCxDxBxDxCxDxA | 2-4 e | DL, XS |
| | AxCxBxCxA | 3-7 d | DL |
| <i>H. metallica</i> | AxDxCxDxBxDxCxDxA | 3-5 e | CL, DL, XS |
| <i>H. vaginalis</i> | AxDxCxDxBxDxCxDxA | eee | CL, DL, XS |
| <i>H. vaginalis</i> ssp. <i>mathiasiae</i> | AxDxCxDxBxDxCxDxA | 2-6 e | CL, DL, XS |
| <i>H. psittacorum</i> | Variable | | |
| | AxDxCxDxBxDxCxDxA | eee | DL |
| | AxCxBxCxA | 3-7 e | DL, XS |
| | AdCdBdCdA | | DL |
| | AcBcA | | DL |
| | AbA | | DL |
| | a only | | DL |
| <i>H. hirsuta</i> | AxDxCxDxBxDxCxDxA | 3-4 e | DL |
| <i>H. indica</i> | AxDxCxDxBxDxCxDxA | 2-5 e | CL, DL, XS |
| Musaceae | | | |
| <i>Musa rosea</i> | AxDxCxDxBxDxCxDxA | 2-5 e | DL, XS |
| <i>Musa velutina</i> | AxDxCxDxBxDxCxDxA | 3-7 e | DL |
| <i>Musa</i> cv. Go Sai Yung | AxCxBxCxA | eee(e)Deee(e)Deee(e)Deee(e) | CL |
| <i>Musa</i> sp. | AxDxCxDxBxDxCxDxA | 3-5 e | DL |
| <i>Ensete</i> sp. | AxDxCxDxBxDxCxDxA | 3-4 e | CL |

*CL, cleared leaf; DL, dry leaf; XS, cross section.

within the longitudinal extent of a single subset. The latter occurs when an e (or f) vein ends in a commissural vein. In *H. chartacea*, immediately adjacent to the costa there is often an increased number of veins in a set, up to ca. 50. These additional veins are typically smaller in size than the e veins.

Even when the assessment of the set is standardized to a single location, there is no single set formula that is common to all species of *Heliconia* (Table 4). However, there is a typical set that characterizes most of the species we studied. This set is AxDxCxDxBxDxCxDxA, where x represents a subset of e veins, with a range of from one to eight veins. An x = fEf pattern is also found as a minor variant in some species. The most common variant of this set pattern consists of ca. 33 veins.

A representative example of a species with the most typical set pattern is *H. chartacea*. In this species, x is a subset of from three to five e veins. The higher numbers of e veins are especially prevalent in the subsets bordering the A veins, where four e veins are common. The widths of typical veins are as follows: A ≈ 0.103 mm, B 0.062 mm, C 0.054 mm, and D ≈ 0.047 mm. The smallest subset (e) ranges in size from 0.023 to 0.040 mm. In this species, the D veins are only slightly larger than the e veins.

Two other variants merit note. First, in *H. pendula*, and in some specimens of *H. latispatha*, there are only four subsets of veins instead of five, i.e., the smallest veins belong to subset d instead of e (Table 4). Second *H. psittacorum* is unique among the study species because of the variability of its set pattern. Within the same individual, and sometimes within the same lamina, a set can vary from that typical for *Heliconia* to a set of only one vein size (Table 4). This was the only species with variation this extreme.

Anatomy

The lamina anatomy of 13 species of *Heliconia* was examined, three of which were also examined by Tomlinson (1959). A description of the general characteristics of the *Heliconia* blade is followed by specific descriptions of the species, where these vary from the general description. We concentrate on those aspects of anatomy that seem to have potential to contribute to tearing of the blade. Cell shapes (rectangular, cuboidal, etc.) are determined from cross sections of the lamina.

General description — Adaxial epidermis simple, of small colorless cells with slightly convex (Fig. 5A), convex, or papillate (Fig. 5B) outer walls; occasionally smaller and with less convex outer walls above the larger veins (Fig. 6); anticlinal walls sinuous (Fig. 7A), or less commonly linear (Fig. 7B); stomates uncommon. Adaxial hypodermis one to two layers of thin-walled cuboidal to rectangular, usually colorless cells; cells increasing in size, and occasionally arranged in two layers, immediately adjacent to A veins (Fig. 8); when two layered, the abaxial cells smaller; cells often much reduced in size above the major vascular bundles (Fig. 8). Mesophyll composed of palisade and spongy layers (Fig. 6). Palisade mesophyll of two to three layers; palisade usually interrupted by the bundle sheaths of A and B veins; number of palisade layers reduced above smaller veins. The palisade accounts for approximately 15-30% of the lamina thickness. Spongy meso-

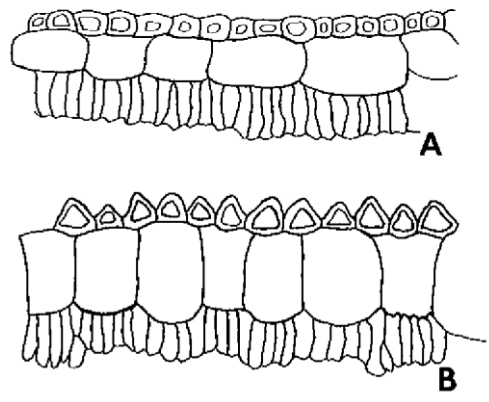


FIG. 5. Drawing of cross sections of the abaxial epidermis, hypodermis, and first layer of the palisade mesophyll. (A) *Heliconia latispatha*, showing slightly convex epidermal cells. (B) *Heliconia metallica*, showing papillate epidermal cells. Scale bar = 0.1 mm.

phyll composed of irregularly lobed cells arranged to form aerenchyma; divided by parenchyma-sheathed commissural veins (Fig. 9A) and, less commonly, by parenchymatous septa (Fig. 9B). The spongy mesophyll accounts for 30-55% of lamina thickness. Vascular bundles varying in size, vessel, phloem, and fiber content across a blade; most larger veins with fiber sheaths both adaxially and abaxially of the conductive tissues; number of layers of fibers decreasing with

bundle size, reduced to zero or one adaxially in the smallest veins; fibers more abundant on the abaxial side of the veins. Veins bordered laterally by large colorless parenchyma cells; rarely extending around the fiber sheaths of the smaller veins. One large tracheal element surrounded by a distinct sheath of parenchyma cells present in A, B, C, and sometimes D veins (Fig. 6). One to three layers of chlorophyllous cells often present between veins and abaxial hypodermis. Abaxial hypodermal cells usually rectangular; interrupted by substomatal chambers and rarely by fiber sheaths of veins. Abaxial epidermis simple, of small colorless cells; outer walls convex or flattened; stomates frequent in the intervascular regions.

Heliconia platystachys

Adaxial epidermal cells convex with sinuous anticlinal walls; cells above A veins smaller and with more flattened outer walls. Adaxial hypodermis mostly one layered; two layers present immediately adjacent to A veins; cells much reduced over A veins, creating a small depression above the vein. Palisade mesophyll ca. 20% of lamina thickness; interrupted by A and B veins; ca. one layer of palisade over C veins. Spongy mesophyll ca. 50% of lamina thickness; divided by parenchyma-sheathed commissural veins and parenchymatous septa. Abaxial epidermal cell walls flat.

Heliconia metallica

Adaxial epidermal cells strongly papillate (Fig. 5B) except over A and occasionally B veins, where cells are more convex; with sinuous anticlinal walls. Adaxial hypodermis mostly one layered, 2-3 cells form a second layer immediately adjacent to A veins; cells slightly reduced over A veins. Palisade mesophyll ca. 15% of lamina thickness; interrupted by A and B veins, or only single layered over these veins; slightly reduced over other veins. Spongy mesophyll ca. 50% of lamina thickness; divided by parenchyma-sheathed commissural veins only. Abaxial epidermal cell walls convex.

Heliconia chartacea (Fig. 6)

Adaxial epidermal cells convex; cells adjacent to A veins larger; those above A veins smaller and with more flattened outer walls; cells over B veins with more flattened outer walls; anticlinal epidermal walls only very weakly sinuous, or non- sinuous. Adaxial hypodermis one layered throughout; cells enlarged adjacent to A veins, reduced over A and B veins, creating a small depression above these veins. Palisade mesophyll ca. 25% of lamina thickness; interrupted by A and B veins; ca. one layered over C veins. Spongy mesophyll ca. 45% of lamina thickness; divided by parenchyma-sheathed commissural veins only. Abaxial epidermal cell walls flat.

Heliconia vaginalis

Adaxial epidermal cells slightly convex; slightly smaller above A veins; with sinuous anticlinal walls. Adaxial hypodermis one layered throughout; cells slightly enlarged adjacent to A veins, reduced over A veins, creating a small depression above these veins. Palisade mesophyll ca. 15% of lamina thickness; interrupted by A veins; reduced and displaced adaxially over B veins. Spongy mesophyll ca. 35% of lamina thickness; divided by parenchyma-sheathed commissural veins only. Abaxial epidermal cell walls flat.

Heliconia vaginalis ssp. mathiasiae

Adaxial epidermal cells slightly convex; smaller above A veins; with sinuous anticlinal walls. Adaxial hypodermis one layered throughout; cells slightly enlarged adjacent to A veins, reduced over A veins, creating a small depression above these veins. Palisade mesophyll ca. 20% of lamina thickness; interrupted by A veins; reduced over 8, C, and D veins. Spongy mesophyll ca. 40% of lamina thickness; divided by parenchyma-sheathed commissural veins only. Abaxial epidermal cell walls convex.

Heliconia indica

Adaxial epidermal cells flat; slightly smaller over A veins; anticlinal cell walls weakly undulate. Adaxial hypodermis mostly one layered, 2-3 cells form a second layer immediately adjacent to A veins; cells much reduced over A and slightly smaller over B veins. Palisade mesophyll ca. 25% of lamina thickness; interrupted by A and B veins; reduced to a single layer over C veins. Spongy mesophyll ca. 35% of lamina thickness; divided by parenchyma-sheathed commissural veins and infrequently by parenchymatous septa (Fig. 9). Abaxial epidermal cells walls flat.

Heliconia psittacorum

Adaxial epidermal cells flat; slightly smaller above A veins; anticlinal walls linear (Fig. 7B). Adaxial hypodermis one layered, with scattered cells forming a broken second layer; second layer mostly found between or directly over smaller veins; when above veins the cells of the hypodermis closely associated with the fibrous bundle sheath; rarely two layered adjacent to A veins; cells smaller and obdeltoid over larger veins; frequently with dark-staining contents. Palisade mesophyll ca. 30% of lamina thickness; interrupted by bundle sheaths of all veins. Spongy mesophyll ca. 30% of lamina thickness; with few air spaces; cells less branched than in most *Heliconia* spp.; divided by parenchyma-sheathed commissural veins and parenchymatous septa. All vascular bundles with extended fibrous sheaths; sheathed bundles extend from adaxial hypodermis through abaxial hypodermis; size variation of bundles relatively small. No chlorophyllous cells between veins and abax-

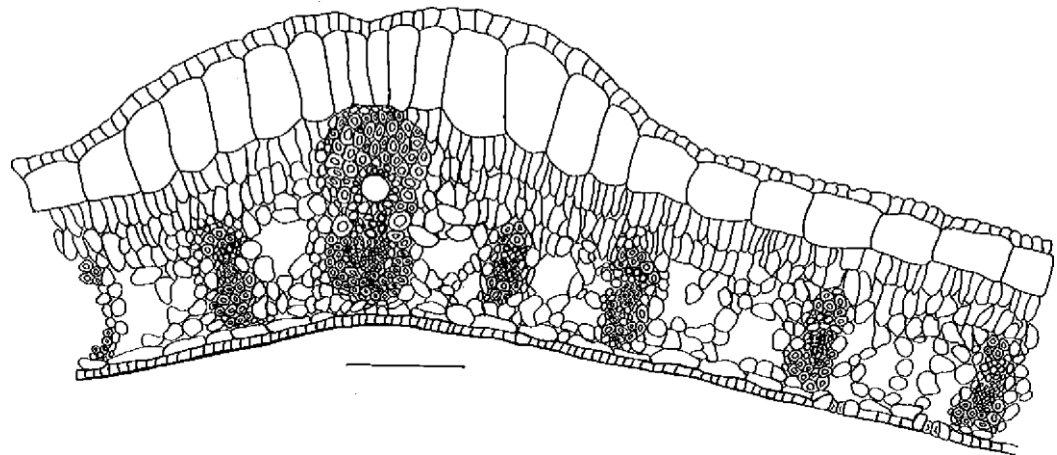


FIG. 6. Drawing of a cross section of *H. chartacea* lamina, showing one A and five e veins. Scale bar = 0.1 mm.

ial hypodermis. Abaxial hypodermis interrupted by all veins. Abaxial epidermal cell walls flat.

Heliconia latispatha

Adaxial epidermal cells slightly convex (Fig. 5A); flattened and larger adjacent to A veins, flattened and smaller above A and B veins; anticlinal walls sinuous. Adaxial hypodermis mostly one layered; 6-7 cells forming a second layer adjacent to A veins; cells larger adjacent to A veins; smaller over A, B, and C veins, creating small depressions above these veins. Palisade mesophyll ca. 30% of lamina thickness; interrupted by A, B, and C veins; reduced to one layer over D veins. Spongy mesophyll ca. 40% of lamina thickness; chlorophyllous cells absent beneath most veins smaller than A; divided by parenchyma-sheathed commissural veins only. Abaxial epidermal cell walls flat.

Heliconia pendula

Adaxial epidermal cells flat; slightly smaller over A veins; anticlinal walls sinuous. Adaxial hypodermis mostly one layered; 1-3 cells form a second layer immediately adjacent to A veins; smaller over A veins, creating a small depression above these veins. Palisade mesophyll ca. 20% of lamina thickness; interrupted by A veins; reduced to ca. one layer over B veins; slightly compressed over other veins. Spongy mesophyll ca. 50% of lamina thickness; divided by parenchyma-sheathed commissural veins and parenchymatous septa. Abaxial epidermal cell walls flattened.

Heliconia stilesii

Adaxial epidermal cells convex with extremely thick walls; anticlinal walls sinuous. Adaxial hypodermis usually one layered throughout; 1-4 cells occasionally forming a second layer adjacent to A veins; cells larger adjacent to A veins; smaller over A veins, forming a small depression above these veins. Palisade mesophyll ca. 30% of lamina thickness; interrupted by A veins; reduced to one layer over B, and compressed over C veins. Spongy mesophyll ca. 50% of lamina thickness; divided by parenchyma-sheathed commissural veins and parenchymatous septa. Abaxial epidermal cell walls flat.

Heliconia stricta

Adaxial epidermal cells convex; slightly smaller over A veins; anticlinal walls sinuous (Fig. 7A). Adaxial hypodermis

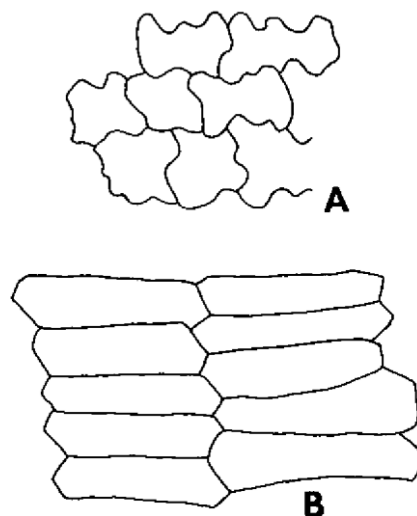


FIG. 7. Surface views of adaxial epidermal cells. (A) *Heliconia stricta*, with undulate anticlinal walls. (B) *Heliconia psittacorum*, with linear anticlinal walls. Scale bar = 0.1 mm.

usually one layered; ca. 5 cells occasionally forming a second layer adjacent to A veins; cells larger and more columnar adjacent to A veins; smaller over A veins, forming a small depression above these veins. Palisade mesophyll ca. 20% of lamina thickness; interrupted by A veins; reduced to one layer over B, and compressed over smaller veins. Spongy mesophyll ca. 35% of lamina thickness; divided by parenchyma-sheathed commissural veins only. Abaxial epidermal cell walls convex.

Heliconia caribaea x bihai

Adaxial epidermal cells convex; smaller and flattened over A veins; anticlinal walls sinuous. Adaxial hypodermis one layered, except adjacent to A veins; ca. 6 cells forming a second layer; cells smaller over B veins, ca 4 x the size of the epidermal cells; much smaller over A veins, ca. 1-2 x size of the epidermal cells. Palisade mesophyll ca. 25% of lamina thickness; interrupted by A and B veins; at least slightly compressed over smaller veins. Spongy mesophyll ca. 50% of lam-

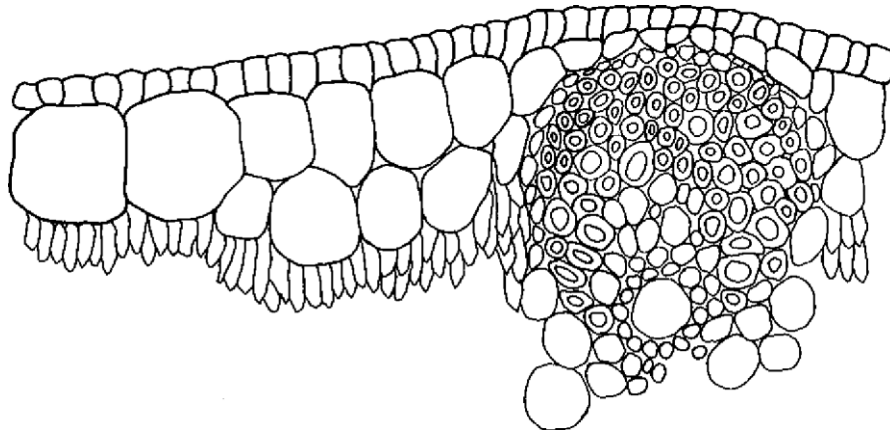


FIG. 8. Drawing of adaxial portion of lamina cross section of *H. caribaea x bihai*. Note the two-layered adaxial hypodermis adjacent to the A vein and the small hypodermal cells over this vein. Scale bar = 0.1 mm.

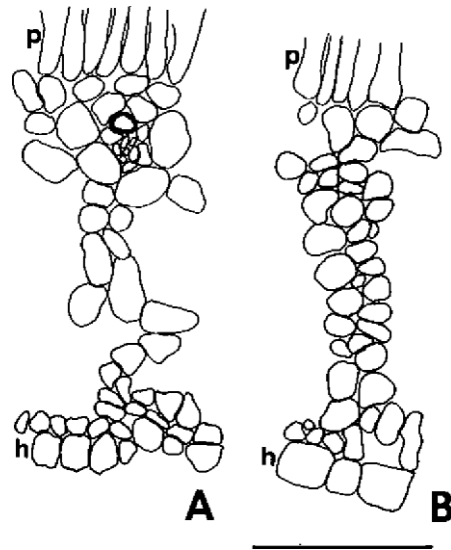


FIG. 9. Drawing of cross sections of septa of spongy mesophyll in *H. indica*. The septa run between the palisade mesophyll (*p*) and the abaxial hypodermis (*h*). Commissural vein with parenchymatous sheath. (B) Nonvascularized, parenchymatous sheath. Scale bar = 0.1 mm.

ina thickness; divided by parenchyma-sheathed commissural veins and parenchymatous septa. Abaxial epidermal cell walls flat.

Heliconia bourgaeana

Adaxial epidermal cells convex; slightly smaller A veins; anticlinal walls sinuous. Adaxial hypodermis one layered throughout; much enlarged approaching A veins; smaller and forming a flattened area over A veins. Palisade mesophyll ca. 30% of lamina thickness; interrupted by A veins; reduced to one layer over B, and at least slightly compressed over smaller veins. Spongy mesophyll ca. 55% of lamina thickness; divided by parenchyma-sheathed commissural veins and infrequently by parenchymatous septa. Abaxial epidermal cell walls flat.

Musaceae

The laminas of the Musaceae are similar in many respects to those of the Heliconiaceae. By virtue of their general shape and vein angles they belong to type 1 laminas, as defined above (Figs. 1A, 1F). However, they differ from the laminas of the Heliconiaceae in that the apex is usually torn and irregular because of the drying and shriveling of the precursory tip (Vorläuferspitze) as the leaf unrolls (Skutch 1927).

The size of one species of *Musa* was measured in this study. The average size of blades of *Musa velutina* (Fig. 1F) is 90 by 30 cm (L x W).

The thickness of the blade of *M. velutina* was also measured from fresh leaves. The average thickness parallel to the veins is 0.260 mm, with a range from 0.204 mm at midleaf near the margin to 0.325 mm at the base of the lamina, near the costa. At the margin, the blades of this species decrease in thickness approaching the midleaf then increase to the base. At the costa, the blade increases in thickness from the apex to base of the lamina. Near the margin, thicknesses parallel to the veins are 0.211 mm (apex), 0.204 mm (midleaf), and 0.212 mm (base). Near the

costa these regions have thicknesses of 0.261 mm (apex), 0.323 mm (midleaf), and 0.325 mm (base).

Vein angles were observed in three species of the Musaceae (Table 3). The range in laminar angle is from 74.2° in *M. velutina* to 81.6° in *Musa* sp. The range of costal angle is 4.1 to 9.4° in these same species, and the range of marginal angles is 7.4° in *Musa rosea* to 16.0° in *Musa* sp.

Set patterns have been investigated in five species of Musaceae. As with the Heliconiaceae, variation was observed both within a blade and between species. However, the majority of the species observed share a common set pattern (Table 4). The typical set pattern for the Musaceae is identical to that of the Heliconiaceae. For example, *M. rosea* has the set pattern $AxDxCxDxBxDxCxDxA$, where $x = 1$ to 3 e veins. Representative widths of the veins in this set are $A = 0.068$ mm, $B = 0.046$ mm, $C = 0.038$ mm, $D = 0.029$ mm, and $e = 0.020$ mm. A distinct set pattern was noted in *Musa* cv. *Go Sai Yung*. This pattern is $AxDxDxDxCxDxDxDxBxDxDxDxCxDxDxDxA$, where $x = 3$ to 4 e veins. This pattern is unique because of the presence of more than one D vein between the veins of the next larger subset.

Anatomy

The laminas of four species of the Musaceae were studied anatomically: three *Musa* spp. and one *Ensete* sp. There are many similarities between lamina anatomy in the Heliconi-

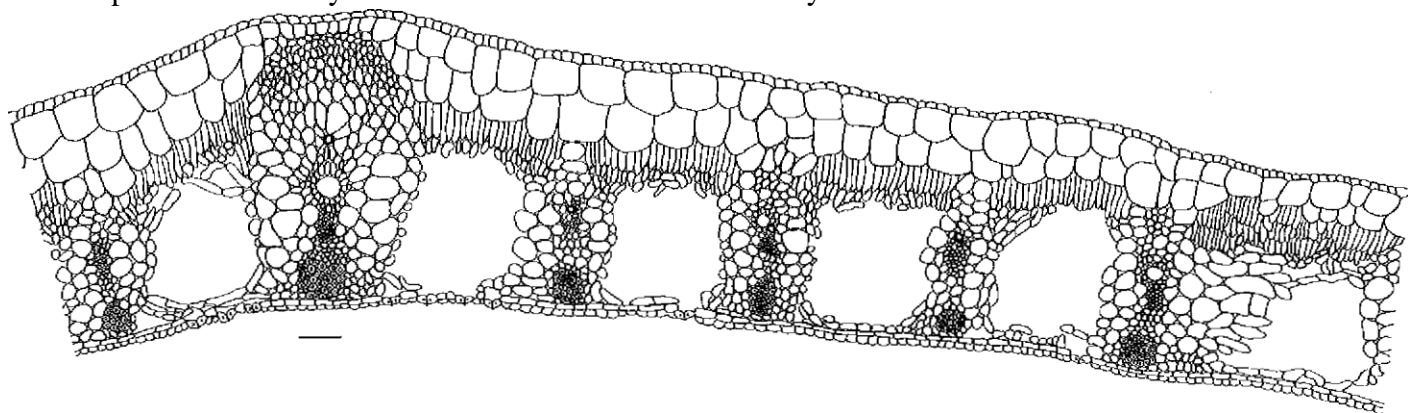


FIG. 10. Drawing of a cross section of *Ensete* sp. lamina, showing one A and five e veins. Note the large cavities in the spongy mesophyll. Scale bar = 0.1 mm.

aceae and that in the Musaceae. A general description of blade anatomy in the family is presented, followed by descriptions of the individual species, where these are different from the general description.

General description — Adaxial epidermis simple, of small colorless cells with convex outer walls; occasionally smaller above the larger veins; anticlinal walls linear; stomates uncommon. Adaxial hypodermis one to two layers of thin-walled cuboidal to rectangular, colorless cells; cells decreasing in size and arranged in two layers approaching the A veins; much reduced in size above the major vascular bundles (Fig. 10); two hypodermal layers occasionally present above smaller veins and between veins. Crystals common in the adaxial hypodermis in some species. Mesophyll composed of palisade and spongy layers. Palisade mesophyll of one to three layers, two to three layers more common adjacent to A veins; cells of most adaxial layer more columnar and more regular in shape; palisade interrupted by the bundle sheaths of all veins (Fig.

10), or interrupted by the larger veins and reduced to one layer above the smallest veins; tanniniferous idioblasts frequently present. The palisade accounts for approximately 25-41% of the lamina thickness. Spongy mesophyll a single layer of irregularly lobed cells lining the large intervascular air cavities (Fig. 10), or less commonly composed of aerenchyma; divided by parenchymatous septa, and by parenchyma-sheathed commissural veins. The spongy mesophyll accounts for 21-58% of lamina thickness. Vascular bundles varying in size, vessel, phloem, and fiber content across a blade; all veins, or all except the smallest veins, with fiber sheaths both adaxially and abaxially of the conductive tissues; number of layers of fibers decreases with bundle size, reduced to zero or one adaxially in the smallest veins (Fig. 10); fibers more abundant on the abaxial side of the veins. Veins bordered laterally by large colorless parenchyma cells; occasionally extending around the fiber sheaths (Fig. 10); enlarged parenchyma cells present adaxially to sheath in some species. One large tracheal element surrounded by a distinct sheath of parenchyma cells present in A, B, and C veins. Laticifers occur in association with the vascular bundles. Abaxial hypodermal cells usually rectangular; interrupted by substomatal chambers; occasionally smaller under fiber bundle sheaths. Abaxial epidermis simple; outer cell walls often convex; stomates frequent in the inter-vascular regions. Raphid sacs occasional throughout.

Musa rosea

Adaxial hypodermis two layered adjacent to A veins and with occasional isolated cells forming a second layer, usually located directly above other veins; prismatic crystals common in cells of the adaxial hypodermis. Palisade mesophyll ca. 41% of lamina thickness; interrupted by fiber sheaths of most vascular bundles, except the smallest veins which lack an extended bundle sheath. Spongy mesophyll ca. 23% of lamina thickness; of irregularly branching and lobed cells forming an aerenchymatic tissue. Bundle sheaths capped by fibers both adaxially and abaxially; parenchyma cells not extending around, or adaxial to, the fiber sheaths.

Musa velutina

Adaxial hypodermis mostly single; isolated or paired hypodermal cells occasional adjacent to A veins and adaxial to smaller veins. Palisade mesophyll ca. 30% of lamina thickness; interrupted by bundle sheaths of all veins. Spongy mesophyll ca. 43% of lamina thickness; of large intervascular spaces lined with chlorophyllous cells. All vascular bundles with extended sheaths; parenchyma cells not extending around, or adaxial to, the fiber sheaths.

Musa cv. Go Sai Yung

Adaxial hypodermis mostly single; isolated or paired hypodermal cells occasional adjacent to A veins and adaxial to smaller veins; fewer isolated cells than in *M. velutina*. Palisade mesophyll ca. 32% of lamina thickness; interrupted by bundle sheaths of all veins. Spongy mesophyll ca. 32% of lamina thickness; of large intervascular spaces lined with chlorophyllous cells. All vascular bundles with extended, fibrous sheaths; parenchyma cells not extending around or adaxially to the fiber sheaths.

Ensete sp. (Fig. 10)

Adaxial hypodermis two layered adjacent to A veins and adaxial to smaller veins. Palisade mesophyll ca. 25% of lamina thickness; interrupted by bundle sheaths of all veins. Spongy mesophyll ca. 58% of lamina thickness; of large intervascular spaces lined with chlorophyllous

cells. Cells of fiber sheaths with thicker walls and more abundant on abaxial side of vascular bundles; parenchymatous bundle sheaths large, extending laterally around and above perivascular fibers.

DISCUSSION

There is considerable variation in lamina shape, size, venation pattern, and anatomy in the Heliconiaceae and Musaceae. However, other than anatomy, none of the characters investigated in this study differentiate between these two families.

Based on this study and a review of the literature, the shape and size of the lamina varies more in the Heliconiaceae than in the Musaceae. Lamina size in the Heliconiaceae ranges from 0.1 to 3(-4) m (Andersson 1985a, 1985b). In the Musaceae, Cheesman (1947, 1948, 1949, 1950) reports blades ranging in size from 1 m to longer than 3 m.

Of the three basic lamina types found in the Heliconiaceae, only one is represented in the Musaceae. The common lamina type (type 1) might equally well be designated *Heliconia*-like or *Musa*-like and consists of large oblong to narrowly oblong blades, with an asymmetrical cordate base, and an acute to slightly acuminate (*Heliconia*) or irregular (*Musa*) apex.

Although lamina size and shape cannot be used to distinguish the families, they may be of use at the generic or sub-generic levels. For example, the blades of *Heliconia* subgenus *Griggsia* are typically large compared with the other members of the genus (190-400 cm by 55-65 cm; Andersson 1985b), and those of section *Zingiberastrum* are much smaller than average (30-40 cm by 7.5-14 cm; Kress 1984; Andersson 1985a). Thus lamina size may aid in the placement of plants into species, sections, or subgenera, but its use as a valid taxonomic character is questionable above this level.

Lamina thickness varies across the blades of individual species in a variety of ways. Skutch (1927) reported an increase in thickness from the margin to the costa in *Musa sapientum*. We confirm this pattern in the Musaceae and Heliconiaceae and describe several patterns of longitudinal variation in thickness. At the costa it is more common for the thickest portion of the lamina to be at the center of the blade, whereas at the margin the thickest portion is most commonly at the base. These thickness relationships most likely play a role in supporting the blade. It would be interesting to correlate thickness patterns with the degree of wind and heat stress to which a blade is exposed. At present, we have no evidence that these architectural features are associated with lamina tearing. The taxonomic value of lamina thickness is not clear from this preliminary study; however, the range of lamina thickness was greater in the Heliconiaceae than in the Musaceae.

Laminar angles are generally correlated with leaf size. Larger leaves have angles approaching 90°, whereas small leaves have laminar angles below 50°. For this reason, vein angles are not useful in distinguishing the families. The costal angles do, however, often distinguish between species.

The Heliconiaceae and Musaceae share a general set pattern of Ax Dx Cx Dx l3x Dx Cx Dx A, where x = 1 to 8 e veins. It may be that measurements of absolute vein size will provide useful

taxonomic characters, as is true in the Zingiberaceae (Hickey and Peterson 1978). This possibility is currently under investigation.

The direction of variation in set pattern is different in the two families. In the Heliconiaceae, variation on the basic set pattern tends to reduction in the number of subsets. For instance, in *H. pendula* there is no size difference between what are referred to as subsets D and e in other species. Consequently, the smallest subset in this species is subset d. With this decrease in the number of subsets there is a corresponding increase in the number of d veins. The size of the set in *H. pendula* is ca. 33 veins, comparable with that of other species. A further reduction in the complexity of the set is seen in *H. psittacorum*. In this species the set may be as simple as AbA or may consist of a veins only. In the Musaceae, set variation tends toward elaboration of the set rather than reduction. *Musa* cv. *Go Sai Yung* (the apple banana of Hawaii) has an elaborated set pattern because of the insertion of more than one eee(e) Deee(e) unit between each C vein (Table 4). This leads to a set that is approximately three times as large as is found in any other species.

Tomlinson (1959) investigates the anatomy of six species of the Heliconiaceae, seven of *Musa*, and three of *Ensete* as part of his investigation of the anatomy of the Musaceae, sensu lato. These observations were extended by 7 species of *Heliconia* and 22 species, or subspecies, of *Musa* for the *Anatomy of the Monocotyledons* series (Tomlinson 1969). The species selected for the present study were chosen to complement those studied by Tomlinson (1959, 1969). Of the 17 species studied here, only two (*H. metallica*, *H. psittacorum*) were investigated by Tomlinson (1959).

In general, this study corroborates Tomlinson's (1959, 1969) description of lamina anatomy in the Heliconiaceae and Musaceae. However, in preparing his summary of anatomical features of *Heliconia* (Tomlinson 1959, Table 6) and his general description of the Anatomy of the Musaceae (Tomlinson 1959, p. 784), Tomlinson does not mention some important anatomical variants. Some of these omissions are due to the species Tomlinson sampled, whereas others are most likely due to his desire to present a general overview of the anatomy of the family. The characters are discussed individually below.

The anticlinal adaxial epidermal walls are usually undulate in *Heliconia*, but linear walls are found in some species. Tomlinson (1959) reports linear walls from *H. rostrata*, and they are reported in *H. psittacorum* in this study. That Tomlinson (1959) did not find linear walls in the latter species, which he studied, may be due to intraspecific variability. There are many cultivars of *H. psittacorum*. Very weakly sinuous or nonsinuous anticlinal walls are found in *H. chartacea* and *H. indica*.

Tomlinson (1959, Table 6; 1969) states that the adaxial hypodermis is always one layered in *Heliconia*. That this is not the case adjacent to the A veins of some species (*H. platystachys*, *H. metallica*, *H. indica*, *H. latispatha*, *H. pendula*, *H. stilesii*, *H. striata*, *H. caribaea x bihai*) has been demonstrated in this study (Fig. 8). Although lacking a second hypodermal layer adjacent to the A veins, *H. psittacorum* has scattered cells forming a second layer between, or directly over, the smaller veins. The lack of a second hypodermal layer is one character Tomlinson (1959) uses to differentiate between *Heliconia* and the other genera of the Musaceae, s.l.

In *Heliconia*, the laminar veins usually have fiber sheaths on both the adaxial and abaxial sides but are not buttressed. An exception is *H. psittacorum*, which has fiber buttresses that run between the adaxial hypodermis and the abaxial epidermis. Tomlinson (1959) notes this variation in his description of the genus but omits it in his family description. This discrepancy is also present in Tomlinson (1969), where he omits mention of the buttresses in *H. psittacorum*.

The spongy mesophyll of *Heliconia* is divided by septa that Tomlinson (1959, 1969) describes as consisting only of parenchyma-sheathed transverse veins (i.e., commissural veins). He does not mention the occurrence of parenchymatous septa, which have been described in a number of species in this paper (*H. platystachys*, *H. indica*, *H. psittacorum*, *H. pendula*, *H. stilesii*, *H. caribaea x bihai*, *H. hourgaeana*). This character is important because Tomlinson (1959) uses the lack of parenchymatous septa to separate the *Heliconia* from the other genera of the Musaceae, s.l.

As Tomlinson (1959, 1969) points out, many of the features of lamina anatomy are common to both the Heliconiaceae and the Musaceae. This suggests a close taxonomic placement of the families. However, a number of anatomical characters make it clear that the families are distinct. The characters listed here are only those that are investigated in this study. Tomlinson (1959) suggests additional characters to differentiate the two families. Although not an absolute difference, the anticlinal walls of the adaxial epidermal cells are more commonly undulate in the Heliconiaceae than the Musaceae. The adaxial hypodermis is also more commonly one layered in the Heliconiaceae, but here the difference is merely one of degree, since the Musaceae generally have a two-layered hypodermis only adjacent to the A veins as do the Heliconiaceae. The lateral extent of the second hypodermal layer is usually greater in the Musaceae, but a second layer consisting of only a few cells, as found in *M. velutina*, is very similar to the second hypodermal layer of many *Heliconia* species. The laminar veins are always buttressed in the Musaceae and generally lack buttresses in the Heliconiaceae, the exception being *H. psittacorum*. The two families also have different structures and amounts of spongy mesophyll. The Heliconiaceae tend to have a more compact spongy mesophyll that may occur as a relatively thin layer of closely arranged cells, as in *H. vaginalis*. The Musaceae are distinguished by the large air spaces that make up the majority of the spongy mesophyll. However, the spongy mesophyll of *M. rosea* is very similar to that of *Heliconia*.

Although Tomlinson's (1959) family summary is excellent as a description of the anatomy of the Musaceae, it cannot be used in a cladistic analysis in which a careful evaluation of primitive and derived states is necessary. Failure to report all the variants in the family description can lead to unwarranted conclusions when data is extracted for a purpose not intended by the author. One of the principles of phylogenetic systematics is that the primitive states for a taxon should be used in determining the higher level relationships of that taxon (Hennig 1966). Therefore, the derived character states within the taxon may be safely ignored when carrying out a higher level cladistic analysis. However, it cannot be concluded that because a character is rare (e.g., fiber buttresses in the Heliconiaceae) it is the derived state (Stevens 1980). This is precisely the conclusion that would be drawn from Tomlinson's (1959) family description of the anatomy of the Musaceae, s.l. To use characters from the literature in a cladistic analysis, the original study should have been done with this type of analysis in mind, or the scientist performing the cladistic analysis should have firsthand knowledge of the characters. We believe that this is a general problem faced by

anyone attempting to extract characters from the literature. Clearly, the author of a paper on systematic anatomy cannot be held responsible for the misuse of his data by others.

An important observation responsible for initiating this study is that many Heliconiaceae and Musaceae blades tear, creating the false pinnae described by Skutch (1927). The mechanism of this phenomenon remains unknown, although Taylor and Sexton (1973) have investigated some of the physiological consequences. Skutch (1927) notes that for *M. sapientum* the tears occur with no correlation to any anatomical feature of the lamina, other than to occur parallel to a vein. He claims that the tear begins at the margin of the lamina and continues inward to as far as the lamina axis (Skutch 1927). The anatomical observation reported by Tomlinson (1959, 1969) and in this paper, reveal no anatomical structures contributing to the disposition to tear, thus supporting Skutch's (1927) observations. Observations of partial tears at Lyon and Waimea arboretums, however, reveal that the tears do not necessarily initiate from the margin, and perhaps more commonly begin within the blade. Further analysis of lamina tearing will involve a statistical analysis of the relationship between lamina size, thickness, laminar angle, and subset pattern to identify those features most correlated with high rates of tearing.

The leaves of the Heliconiaceae and Musaceae have a complex and interesting architecture. The morphological features presented in this study demonstrate that descriptive characters, formerly given scant attention in these and other monocots, can be elicited from the leaves. Further investigation of these characters will explore their usefulness in the study of the phylogeny of the Zingiberales and in the study of mechanical properties, such as leaf tearing.

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